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Two new taxa of Leptodirini (Coleoptera: Leiodidae, Cholevinae) from the Cantabrian cornice (Asturias, Spain). Biogeographical observations

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Two new taxa of Leptodirini (Coleoptera: Leiodidae, Cholevinae) from the Cantabrian cornice (Asturias, Spain). Biogeographical observations. - *Quaestus (Asturianella) incognitus* subgen. n., sp. n, and *Quaestus (Speogeus) mermejaensis* sp. n. are described from caves located in the eastern foothills of the Sierra Mermeja (Asturias, Spain). Both taxa are included in the section *Quaestus* (sensu Salgado, 2000). Keys for a better, more precise placement of the new taxa are also given as well as biogeographical observations and a study on colonization by the species captured in the four caves examined in this paper, in comparison with other morphologically similar species or those living in neighbouring areas.

Key-words: Coleoptera - Leiodidae - Leptodirini - taxonomy - *Quaestus (Asturianella) incognitus* sp. n. - *Quaestus (Speogeus) mermejaensis* sp. n. - caves - colonization.

INTRODUCTION

One of the karstic areas with the largest troglobitic fauna stretches over a series of small mountain ranges situated towards the south of Asturias comprising the Crespón, Mermeja, Corteguero, Pintacanales, Ques and Giblaniella sierras. They cover an area of approximately 600 km^2 between the Ponga, Sella, Infierno, Marea, Nalón, S. Isidro and Aller river basins (fig. 27). Eleven species of troglobitic Leptodirini are known from this area. They have been described over the last 20 years (Salgado, 1982, 1984, 1985, 1988, 1989) and are at different stages of evolution, indicating that the caves were colonized during different glacial periods in the Pleistocene.

Undoubtedly, the presence of such a high number of species in such a small area is explained by the occurrence of great orogenic convulsions causing the formation of small mountain ranges and numerous faults, landslides, overthrusts, etc. Well-isolated areas were formed and this interrupted the genetic flow of the populations, the main reason for speciation, which in this case is clearly allopatric (Bellés & Martínez, 1980; Galán, 1993; Salgado, 1995; Peck, 1998).

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In one of the previously-mentioned mountain ranges, the Mermeja, various samplings were carried out intermittently in 4 caves. A known species, *Quaestus (Quaestus) longicornis* (Salgado, 1989) was captured together with one proximate to *Q. (Q.) jeannei* (Coiffait, 1965) and *Q. (Q.) recordationis* (Salgado, 1982), *Quaestus (Quaestus)* sp., this last species is still under study, due to the complexity of its structures and distribution. Two new taxa, *Quaestus (Asturianella) incognitus* subgen. n., sp. n. and *Q. (Speogeus) mermejaensis* sp. n. were also captured.

TAXONOMIC TREATMENT

Description of the new subgenus of the genus *Quaestus*

Asturianella subgen. n.

Type species: *Quaestus (Asturianella) incognitus* sp. n.

Diagnosis. The basic distinguishing characters are: antennal segments of club longer than wide; pronotum strongly transverse, parameres with 4 apical setae; very long, robust stylet with subrectangular basal plate; spermatheca with small spherical apical lobe, basal lobe highly developed and oblong, spermathecal duct long and fine.

Description. Ovoide, anophthalmic; small, less than 3 mm (fig. 1). Antennae not surpassing half body length, all segments longer than wide (fig. 6). Elliptical elytra following curve of prothoracic sides. Mesosternal carina developed, with rounded tip and expanded ventral margin (fig. 9). Legs short. Male protarsi with 4 clearly dilated segments (fig. 7); females with gracile 4-segmented protarsi.

Aedeagus robust, weakly arcuate but with apex strongly curved towards ventral face. Ventral lamina of tegmen slightly wider than long. Parameres somewhat longer than median lobe, distally forming dilated club with 4 setae inserted. Internal sac with two bands almost the same length as sac; long developed stylet inserted in subrectangular basal plate, no other sclerotized pieces discernible, only scales in basal region and fine spines and pilosity near median region (figs 2, 3 and 5).

Apical lobe of spermatheca small and spherical, basal lobe expanded and long spermathecal duct weakly dilated along anterior region (fig. 4).

Etymology. The subgeneric name is a reference to Asturias, the region of Spain where the specimens belonging to this new taxon were captured. The name is of feminine gender.

Discussion. Some of the characters of the external morphology of the new taxon, including, 8th, 9th and 10th segments scarcely long; pronotum transverse with uniformly arcuate sides, elytra quite narrow in posterior region, and in particular, the genitalia, with a well-developed stylet and the spermatheca exhibiting an easily-distinguishable spherical apical lobe, are also observed in the genus *Quaestus*. However, there is one unique and completely distinguishing character in this new taxon, the 4 setae in the apical region of the parameres, which is only present in the genus *Speocharinus* Español & Escolà, 1997, as all the *Quaestus* have only 3. In exceptional cases some specimens may exhibit 4 setae, as indicated by Bellés (1977) in *Quaestus (Quaesticulus) minos* (Jeannel, 1909) and Salgado (1982) in *Quaestus (Quaestus) jeannei* (Coiffait, 1965), both species have a supernummary seta, but it is only present in one specimen and on one paramere.

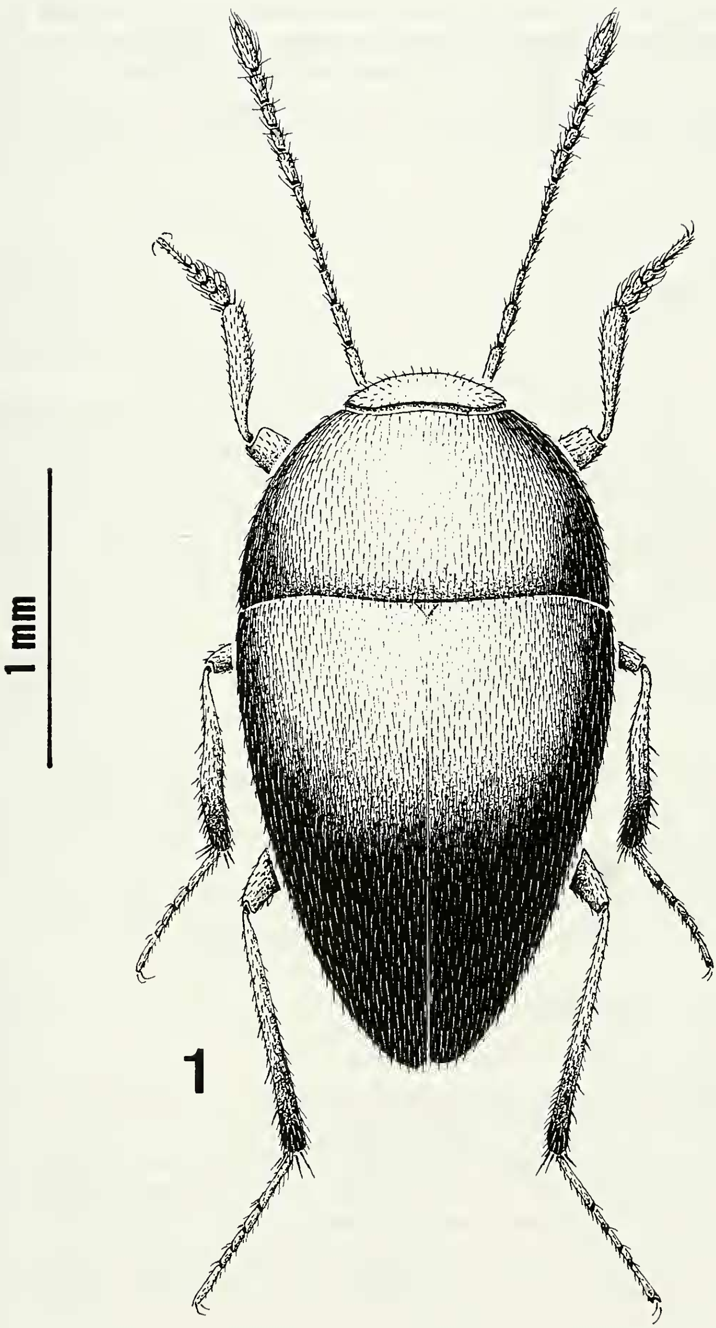


Fig. 1
Quaestus (*Asturianella* subgen. n.) *incognitus* sp. n. (paratype, male), habitus.

Considering the importance of this character, 4 setae in the parameres, with 3 setae never being observed in any specimen, and considering that the aedeagus and spermatheca are quite similar to those in specimens belonging to *Quaestus*, especially the group *jeannei* (Salgado, 1982), the category of genus should not be assigned to this new taxon. The category of monospecific subgenus is sufficient to establish its taxonomic independance.

Taxonomy and key of the subgenera belonging to the genus *Quaestus*

The section *Quaestus* (Salgado, 2000) includes the following valid genera: *Breuilia* Jeannel, 1909; *Breuilites* Salgado, 1980; *Cantabrogeus* Salgado, 2000; *Espanoliella* Guéorguiev, 1976; *Leonesiella* Salgado, 1996; *Quaestus* Schaufuss, 1861; *Oresigenus* Jeannel, 1948 and *Speocharinus* Español & Escolà, 1997.

The genera belonging to this section are characterized by the long elevated or low mesosternal carina (short in the subgenus *Speogeus* only). Internal sac of aedeagus with pilosity, scales, spinules, spines, sclerotised plates or generally long stylet, or a combination of all these structures. Spermatheca with generally discernible basal lobe, more developed than spherical apical lobe. The species belonging to these genera are found along the Cantabrian cornice, except for *Quaestus (Quaesticulus) cisnerosi* (Pérez-Arcas, 1872) which inhabits the Central Mountain Range of the Iberian Peninsula.

Using studies by Salgado (1985, 1993, 2000), Newton (1998) and Perreau (2000) as a basis, the genus *Quaestus* includes 6 subgenera.

1 Elytra lacking sutural striae or with very rudimentary weakly discernible stria, only visible in anterior region of elytrum. Stylet of internal sac of aedeagus bearing plate or basal bowl. Spermatheca with small apical lobe and generally long, fine spermathecal duct 2

1' Elytra with sutural stria along all the elytrum, usually easily discernible. Sylet of internal sac of aedeagus lacking plate or basal bowl. Spermatheca with big or small apical lobe and short spermathecal duct 4

2 Parameres bearing 4 setae in apical region . . . . *Asturianella* subgen. n.

2' Parameres with 3 setae in apical region 3

3 Mesosternal carina short, if the apophysis is near the end of the metasternum, the carina is always low. Angle of carina strongly obtuse. Ventral edge of carina always narrow. Mid posterior region of metasternum often bearing small fovea . . . . *Speogeus* Salgado, 1985

3' Mesosternal carina long and elevated, apophysis always reaching metasternum. Angle of carina just over 90°. Ventral edge narrow or wide. Mid posterior region of metasternum lacking fovea . *Quaestus* Schaufuss, 1861

4 Apical region of elytra pointed and diverging. Median lobe of aedeagus strongly expanded in mid region, with carina in ventral face. Internal sac lacking fanerae, only stylet present . . . . *Samanolla* Salgado, 2000

4' Apical region of elytra rounded and not diverging. Median lobe of aedeagus not strongly expanded in mid region, lacking carina in ventral face. Internal sac with fanerae and stylet 5

5 Male metafemur with small denticle on posterior margin. Internal sac of aedeagus with robust teeth and spines, spinules or both . . . . *Amphogeus* Salgado, 2000

5' Male metafemur lacking denticle in posterior margin. Internal sac of aedeagus with more or less developed spiny formations . . . . *Quaesticulus* Schaufuss, 1861

Descriptions of the new species

Quaestus (Asturianella) incognitus sp. n.

Type material. Holotype, ♂, Cave of Julió, Caleao, T. M. de Caso (Asturias), 31-VII-2002, J.M. Salgado leg., in Muséum d'histoire naturelle de Genève. Paratypes: 48 ♂♂ and 74 ♀♀, same data as Holotype. Cave of the Prau, Puente de Piedra-Buspriz, T. M. de Caso (Asturias), 17-VI-1989, 60 ♂♂ and 96 ♀♀; 28-X-1989, 68 ♂♂ and 73 ♀♀; 31-VII-2002, 3 ♂♂ and 10 ♀♀, J.M. Salgado and D. Rodríguez leg. Cave of Carretera, Puente de Piedra-Buspriz, T. M. de Caso (Asturias), 28-X-1989, 2 ♂♂ and 3 ♀♀, J.M. Salgado and D. Rodríguez leg. Cave of Rearco, Coballes, T. M. de Caso (Asturias), 22-IV-1989, 33 ♂♂ and 50 ♀♀; 15-IV-2003, 45 ♂♂ and 41 ♀♀, J.M. Salgado and D. Rodríguez leg. Muséum d'histoire naturelle de Genève; J.M. Salgado Coll., Dpto. de Biología Animal, Universidad de León (Spain); J. Fresneda Coll., Lleida (Spain); P.M. Giachino, Museo Regionale di Scienze Naturali, Torino (Italy); Museo de Zoología de Barcelona (Spain); Muséum National d'Histoire Naturelle, Paris (France); Field Museum of Natural History, Chicago (USA).

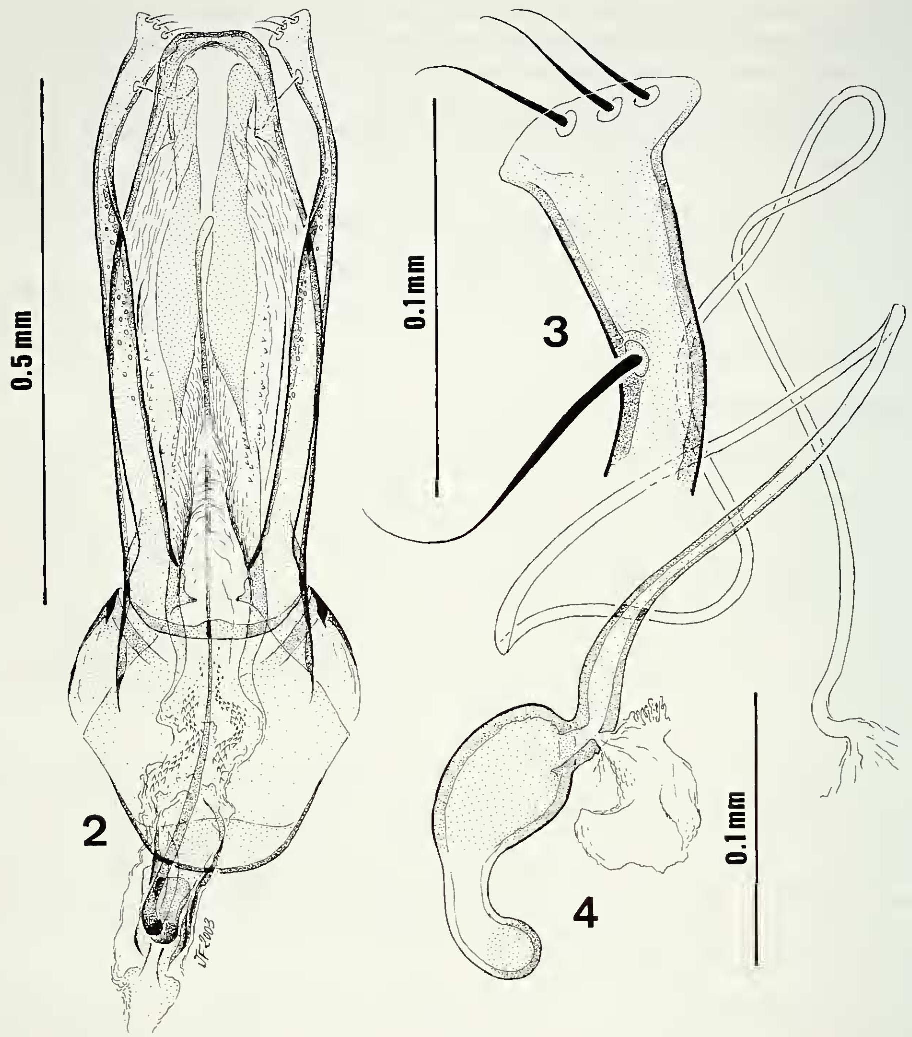
Diagnosis. 11th antennal segment twice the length of 10th; 8th, 9th and 10th segments slightly longer than wide; male protarsi as wide as maximum width of tibia; aedeagus with tip of median lobe curved towards ventral face; parameres somewhat longer than median lobe, with 3 short apical setae and one longer preapical seta; internal sac of aedeagus exhibiting pilosity, scales and very long robust stylet with sub-rectangular basal plate; spermatheca with small spherical apical lobe, and wide oval basal lobe, spermathecal duct very long.

Description. Male. Holotype ♂, 2.56 mm (paratypes: 2.53-2.70 mm). Elongate, elliptic body, not very narrow posteriorly (fig. 1). Uniformly reddish-brown. Shiny tegumenta. Antennae not surpassing half the body length, segments noticeably expanded from 7th (fig. 6). Of particular interest is the 11th segment which is twice the length of 10th; 8th, 9th and 10th segments slightly longer than wide; 3rd and 5th segments equal and slightly longer than 4th and 6th, which are the same (Table I).

Pronotum strongly transverse (maximum width/maximum length relationship: 2.05), sides uniformly arcuate and widest at base. Elytra elongate, less than one and a

Table I. Maximum lengths (L) and widths (W) of antennal segments (1 mm = 50 units).

Segments	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
L	6.5	7.0	5.0	4.0	5.0	4.0	5.5	3.2	4.1	3.9	8
W	2.5	2.7	2.0	2.0	2.0	2.0	2.8	2.4	3.1	3.3	3.6



FIGS 2-4
Quaestus (A.) incognitus sp. n.: (2) aedeagus, dorsal view; (3) apical region of the paramere; (4) spermathecal complex.

half times width of pronotum, margins continuous, gradually narrowing towards tip. Sutural stria absent. Mesosternal carina elevated, apophysis reaching metasternum; obtuse angle with rounded tip and ventral margin wide (fig. 9). Legs slender, moderately long, with first segment of protarsi as wide as maximum width of protibiae (fig. 7).

Aedeagus robust and long (0.77 mm), in dorsal view, median lobe with sides almost parallel as far as apical fourth then narrowing progressively, apical area weakly truncate (fig. 2). In lateral view distal region in extended pointed tip and curved towards ventral part (fig. 5). Parameres just surpassing tip of median lobe, apical region expanded, resembling an axe, with 4 setae inserted, 3 short equal ones in apical margin, a more robust one in club base near internal margin (fig. 3). Long robust stylet of internal sac with subrectangular basal plate, flanked by two thin very weakly sclerotized plates; scales near basal region set out in shape of an arch, fine spinules and pilosity in two narrow rows near median region. Two reinforcement bands almost as long as sac (fig. 2).

FEMALE. As robust as male, with shorter antennae and proportionally thicker segments (Table II). Protarsi not expanded and tetramere. Eighth urite with short, narrow spiculum ventrale, twice as short as length of sternite (fig. 8). Spermathecal complex showing a spermatheca with very small spherical apical lobe, basal lobe twice as wide and almost three times longer than apical lobe; the joining between these lobes short, narrow and not sclerotized; spermathecal duct long, approximately 9 times as long as spermatheca which is slightly expanded in one third of its anterior length (fig. 4).

TABLE II. Maximum lengths (L) and widths (W) of antennal segments (1 mm = 50 units).

Segments	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
L	5.7	6.2	4.0	3.7	4.0	3.7	5.0	2.7	4.0	3.8	7.5
W	2.5	2.7	2.0	2.0	2.0	2.0	2.7	2.3	3.0	3.2	3.6

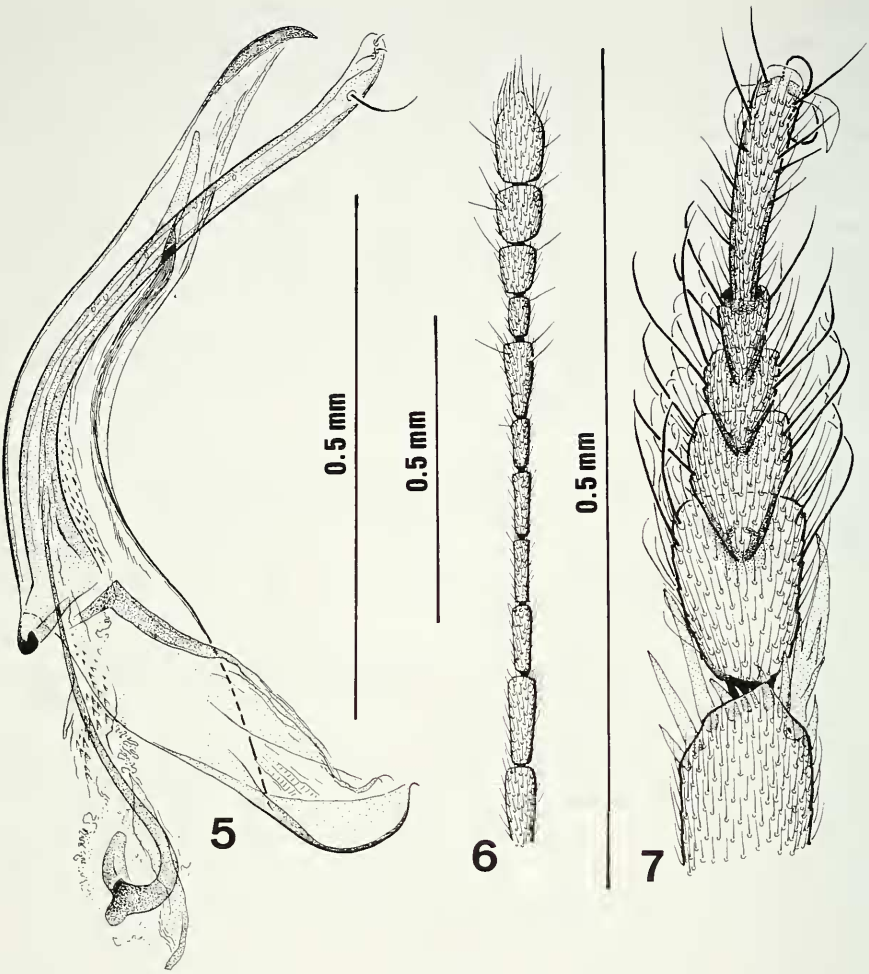
Etymology. "Incognitus=unknown" refers to the long period of time that passed from when this new species was first captured (22-IV-1989) until it was described.

Discussion. This new taxon shows certain similarities to two species in the group *jeannei, Quaestus (Quaestus) jeannei* Coiffait, 1965 and *Q. (Q.) recordationis* Salgado, 1982, in their external morphology, shape of the median lobe, structures of the internal sac of the aedeagus and shape of the spermatheca (figs 10-17). *Q. (Asturianella) incognitus* sp. n. is differentiated from the two previously-mentioned species by the more slender antennal segments, all of which are longer than wide, and a more transverse pronotum; also, the median lobe of the aedeagus is more robust and has a slightly truncate apical area, more parallel sides in the median region and the apical curvature more pronounced. However, two characters make this new species unmistakeable and clearly distinguish it from any other species in the genus *Quaestus*, the shape of the club of the parameres and the 4 setae inserted.

Finally, it should be mentioned that the antennal segments of the specimens captured in the Rearco cave are slightly longer than those of the specimens captured in the other three.

Quaestus (Speogeus) mermejaensis sp. n.

Type material. Holotype, ♂. Cave of the Prau, Puente de Piedra-Buspriz, T. M. de Caso (Asturies, Spain), 17-VI-1989, J.M. Salgado leg., in Muséum d'histoire naturelle de Genève. Paratypes: Cave of the Prau, Puente de Piedra-Buspriz, T. M. de Caso (Asturies, Spain), 17-VI-1989, 35 ♂♂ and 47 ♀♀; 31-VII-2002, 10 ♂♂ and 10 ♀♀, J.M. Salgado and D. Rodríguez leg. Cave of the Carretera, Puente de Piedra-Buspriz, T. M. de Caso (Asturies, Spain), 28-X-1989, 2 ♂♂ and 4 ♀♀, J.M. Salgado and D. Rodríguez leg. Cave of Rearco, Coballes, T. M. de Caso (Asturies, Spain), 22-IV-1989, 2 ♂♂ and 2 ♀♀; 15-IV-2003, 4 ♂♂ and 12 ♀♀, J.M.



Figs 5-7

Quaestus (A.) incognitus sp. n.: (5) aedeagus, lateral view; (6) antenna; (7) protarsum, dorsal view.

Salgado and D. Rodríguez leg. Muséum d'histoire naturelle de Genève; J.M. Salgado Coll., Dpto. de Biología Animal, Universidad de León (Spain); J. Fresneda Coll., Lleida (Spain); P.M. Giachino, Museo Regionale di Scienze Naturali, Torino (Italy); Museo de Zoología de Barcelona (Spain); Muséum National d'Histoire Naturelle, Paris (France); Field Museum of Natural History, Chicago (USA).

Diagnosis. A species of the tribe Leptodirini characterized by: elongate weakly convex body; 8th antennal segment transverse, 9th and 10th segments slightly longer than wide; elytral margins parallel along mid region; mesosternal carina low and short with narrow ventral edge and strongly obtuse angle; parameres clearly surpassing tip of median lobe, dilated club with 3 setae and one or two easily discernible piliferous pores.

Description. MALE. Holotype ♂, 2.62 mm (paratypes: 2.58-2.82 mm). Body elongate, elliptical weakly convex, reddish-brown and covered in short laid back yellowish pilosity. Antennae quite long, clearly surpassing half body length (fig. 23); 11th segment three times longer than wide and three times as long as 10th segment; 8th segment transverse; 3rd to 6th segments similar in length (Table III).

TABLE III. Maximum lengths (L) and widths (W) of antennal segments (1 mm = 50 units).

Segments	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
L	7.2	8.0	5.1	4.9	5.0	5.0	6.4	3.0	4.1	4.0	11.7
W	2.7	2.4	2.0	2.0	2.0	2.0	3.4	3.0	3.7	3.8	4.0

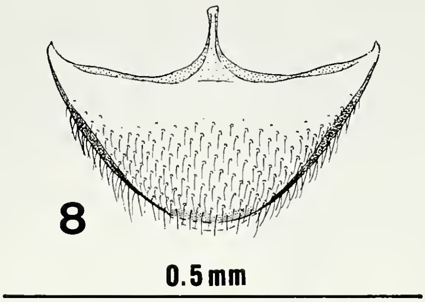
Pronotum transverse, almost twice as wide as long (1.88), sides uniformly curved, attenuated towards front and weakly narrow towards back; basal area as wide as elytra. Elytra elongate,1.65 times longer than wide, with parallel margins along two thirds of their length, gradually narrowing to the tip. Sutural stria not discernible. Mesosternal carina low, with very obtuse angle and very rounded tip; ventral margin narrow, apophysis slightly surpassing mesosternum (fig. 21). Legs slender and quite long, protarsi dilated, the first being wider than the maximum width of the protibiae (first protarsi/protibiae ratio = 1.25).

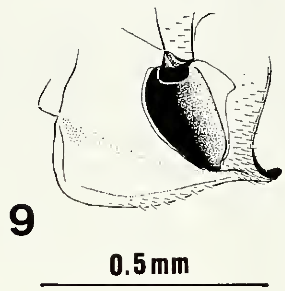
Aedeagus weakly wide and quite long (0.60 mm) in lateral view, with uniformly arcuate median lobe and curved pointed tip (fig. 22). In dorsal view, tip of median lobe truncate and slightly arcuate inwards in median region (fig. 18). Parameres clearly surpassing tip of median lobe, with expanded shovel-like club, internal margin pointed, resembling a peak; of the three setae inserted in the club, the lower one is long and inserted in the base, fairly distant from the two small apical ones, with insertion pores close together and one or two pores above the apical setae which have no setae (fig. 19). Internal sac with numerous weakly-sclerotised scales scattered in mid basal region; stylet very long and fine, almost as long as median lobe, with well-developed subrectangular insertion plate. Two reinforcement bands as long as internal sac (fig. 18).

FEMALE. Generally a little more robust than male, with elytra slightly more convex. Antennae somewhat shorter and segments comparatively thicker than in male (Table IV). Spiculum ventrale of 8th urite very short and narrow, 3 times shorter than length of sternite. Spermathecal complex with spermatheca quite rectilinear, apical lobe small and spherical, basal lobe much longer than wide, both well-sclerotised, the joining region more narrow and translucent; spermathecal duct fine, just over 4 times as long as spermatheca, and slightly more expanded along anterior fifth (fig. 20).

TABLE IV. Maximum lengths (L) and widths (W) of antennal segments (1 mm = 50 units).

Segments	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
L	6.9	7.8	5.0	4.7	5.0	4.8	6.0	2.8	4.0	4.0	9.0
W	2.7	2.5	2.1	2.1	2.1	2.1	3.5	2.8	3.7	3.8	4.0



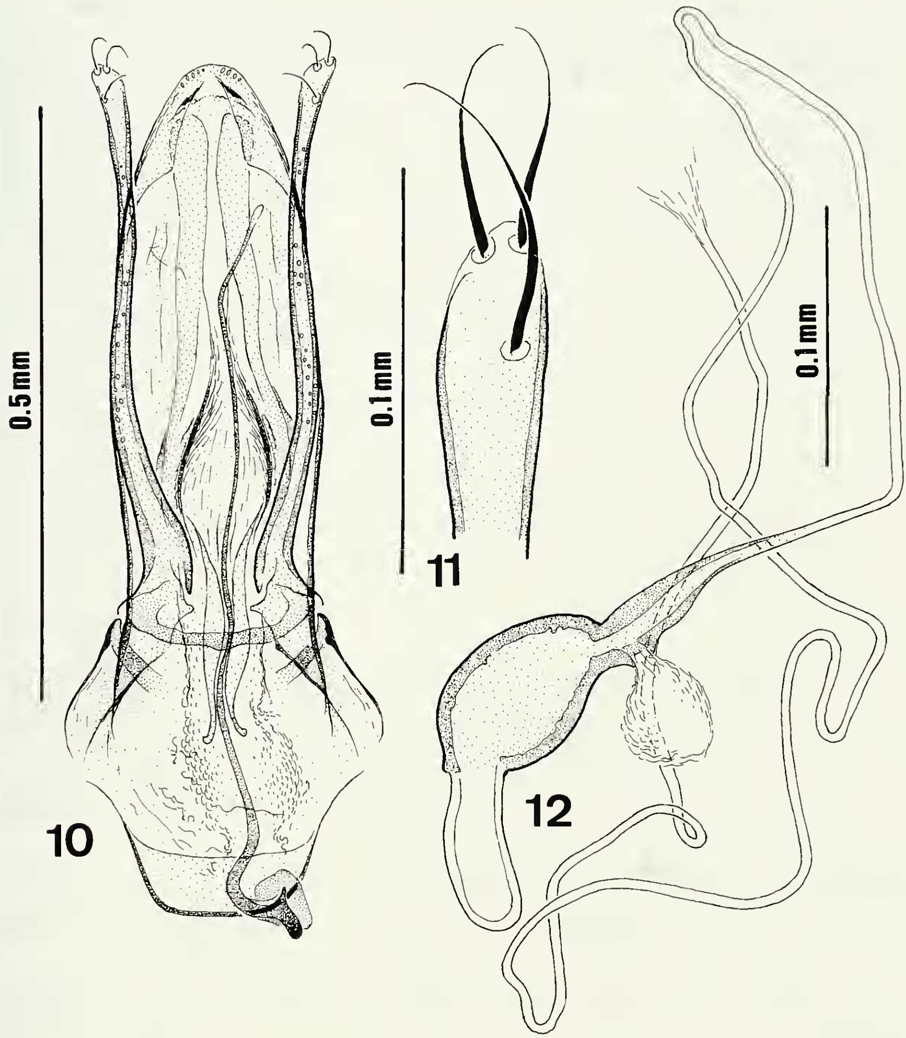


Figs 8-9

Quaestus (A.) incognitus sp. n.: (8) urite female, ventral view; (9) mesosternal carina, lateral view.

Etymology. The name refers to the caves situated in the foothills of the Sierra Mermeja where specimens belonging to this new species were found.

Discussion. The only species that *Quaestus (Speogeus) mermejaensis* sp. n. could be mistaken for is *Q. (S.) nietoi* (Salgado, 1988) as they are similar morphologically. There are, however, constant and significant differences in some external morphological characters and in the genitals. These differences are: 8th antennal segment in *Q. (S.) mermejaensis* transverse, 9th and 10th slightly longer than wide; apophysis of mestosternal carina only just surpassing mesosternum; parameres widely surpassing median lobe, insertion pores of both apical setae more separated, pore of basal seta at a considerable distance. Whilst all the antennal segments in *Q. (S.) nietoi* are clearly longer than wide, the apophysis of the mesosternal carina almost reaches the metasternum, the club of the parameres has a different shape and only just surpasses the tip of the median lobe, the insertion pores of the apical setae are closer together and the insertion pore of the basal seta is slightly separated (figs 24, 25); finally, the area joining the spermathecal lobes is shorter and the spermathecal duct is clearly longer (fig. 26). Added to all this, the populations of these species are isolated by barriers such as overthrusts and sandstone areas separating them, as can be seen on the distribution map (fig. 27).



Figs 10-12

Quaestus (Quaestus) jeannei (Coiffait, 1965): (10) aedeagus, dorsal view; (11) apical region of the paramere; (12) spermathecal complex.

KEY TO THE SPECIES OF THE SUBGENUS *SPEOGEUS*

1 Basal plate of stylet of internal sac rounded 2
1' Basal plate of stylet of internal sac subrectangular 3

2 Male protarsi more narrow or slightly wider than maximum width of protibiae; 11th antennal segment 3 times or just over 3 times as long as 10th; parameres narrow, with tip in the shape of an oblong club . . . . *Q. (S.) amicalis* (Salgado, 1984)

2' Male protarsi almost twice as wide as maximum width of protibiae; 11th antennal segment at most 2.5 times as long as 10th; parameres wide, tip curved and club barely differentiated . . . . *Q. (S.) littoralis* Salgado, 1999

3 Parameres longer than median lobe, with club flattened and more or less pointed towards inner side 4
3' Parameres as long as or slightly shorter than median lobe, with tip rounded and lacking distinguishable club 5

4 8th, 9th and 10th antennal segments clearly longer than wide; apophysis of mesosternal carina reaching or just surpassing mid region of mesosternum; parameres slightly surpassing tip of median lobe; distance between the two apical setae of club of parameres less then three times the distance between them and insertion point of lower seta . . . . *Q. (S.) nietoi* (Salgado, 1988)
4' 8th antennal segment transverse, 9th and 10th segments slightly longer than wide; apophysis of mesosternal carina not reaching mid region of mesosternum; parameres widely surpassing tip of median lobe; distance between the two apical setae of club of parameres almost 5 times the distance between them and insertion point of lower seta . . . . *Q. (S.) mermejaensis* sp. n.

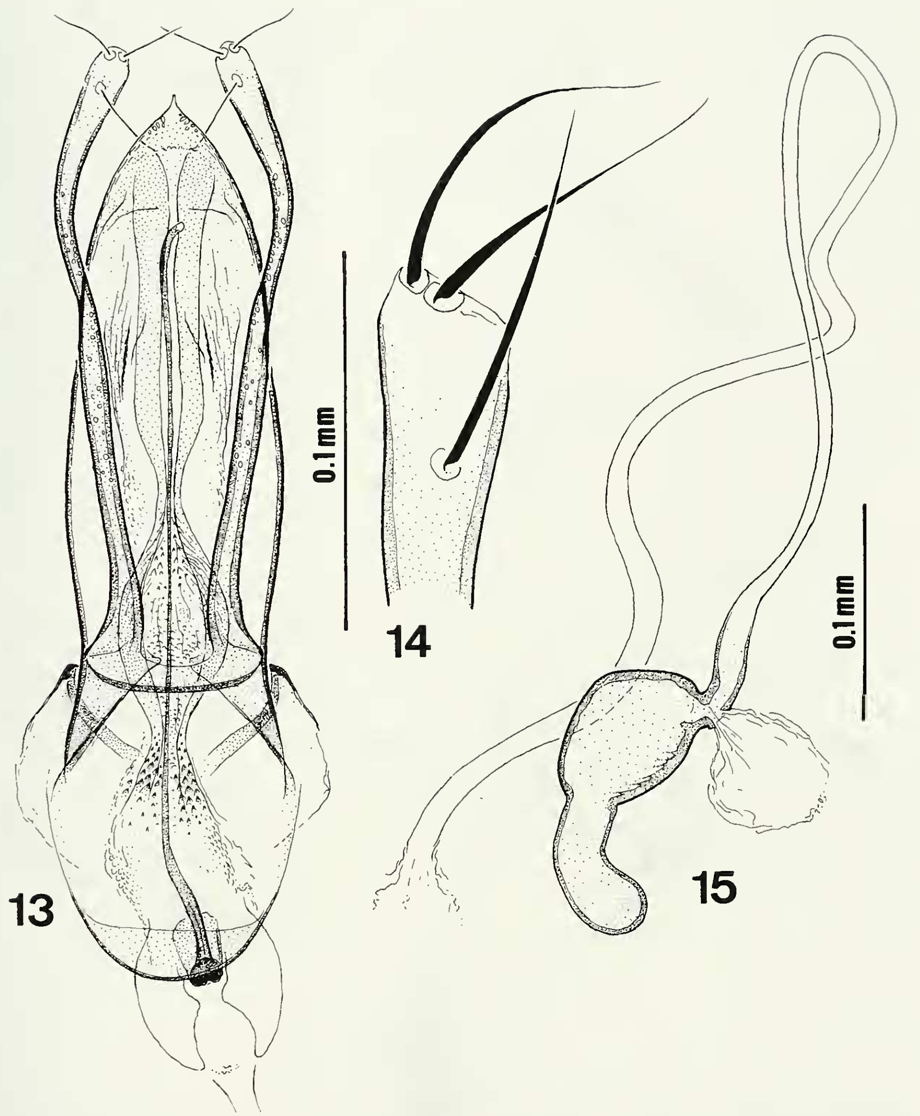
5 3 setae of parameres inserted in apical region of club; mid-apical region of internal sac lacking developed fanerae . . . *Q (S.) avicularis* (Salgado, 1985)
5' 3 setae of parameres not inserted in apical region of club, one inserted near base; mid apical region of internal sac with two or three groups of well-developed fanerae . . . . *Q. (S.) diegoi* (Salgado, 1989)

BIOLOGICAL AND ECOLOGICAL OBSERVATIONS

The following is a description of some of the characteristics of the four caves sampled in this study.

Julió cave (UTM: 30TUN023803). This cave is situated 1000 m. in a limestone area from the Carboniferous period. It is surrounded by *Corylus avellana* L. and *Fagus sylvatica* L. as the predominating plant species, with a rocky area nearby. It is 800 m long and easy to enter and walk through. The first 50 m are highly eroded and there is a large clay substrate. Facing south-east, the temperature inside is 12° C (summer) with 97-98% relative humidity above the first 50 m. Most of the catches were carried out randomly at between 50 and 150 m in heaps of organic plant material and scattered bat faeces and using attraction traps (cheese, fruit, liver). *Q. (A.) incognitus* sp. n. cohabits with *Q. (Q.) longicornis*. The populations of the latter species are also found in caves in the bordering area of the Sierra del Crespón.

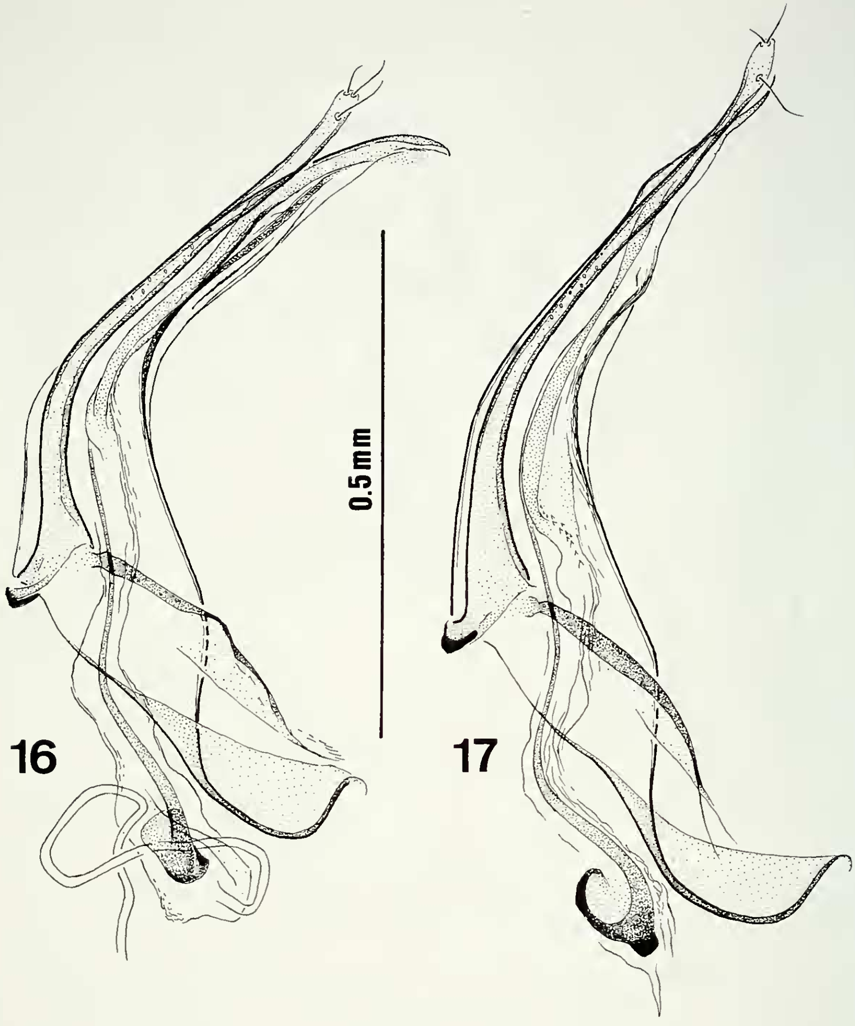
Prau cave (UTM: 30TUN055824). Situated at 815 m., also in limestone areas from the Carboniferous period. The mouth of the cave faces south and the surrounding area is predominated by *Quercus robur* L., *Alnus glutinosa* (L.) Gaertn. and *Corylus avellana* L. It is an active cave still in the process of formation and approximately 200



Figs 13-15
Quaestus (Q.) recordationis (Salgado, 1982): (13) aedeagus, dorsal view; (14) apical region of the paramere; (15) spermathecal complex.

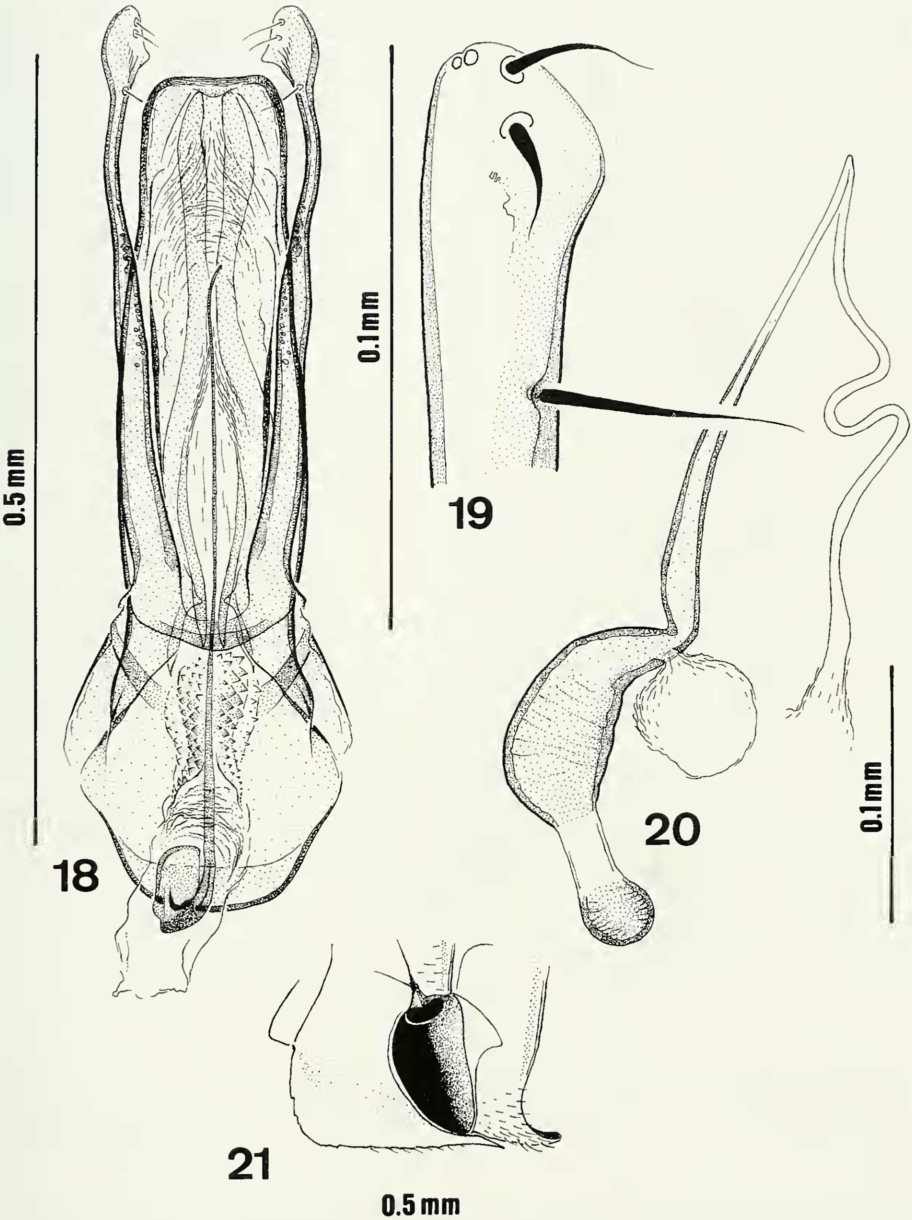
m long. A number of stalactites, stalagmites and outflows can be seen inside. The temperature is between 8° C (winter) and 11° C (summer), with 98.5% constant relative humidity.

As the ground is free from organic material and there are a number of gours, catches were only possible using attraction and pit fall traps, especially in the centre of



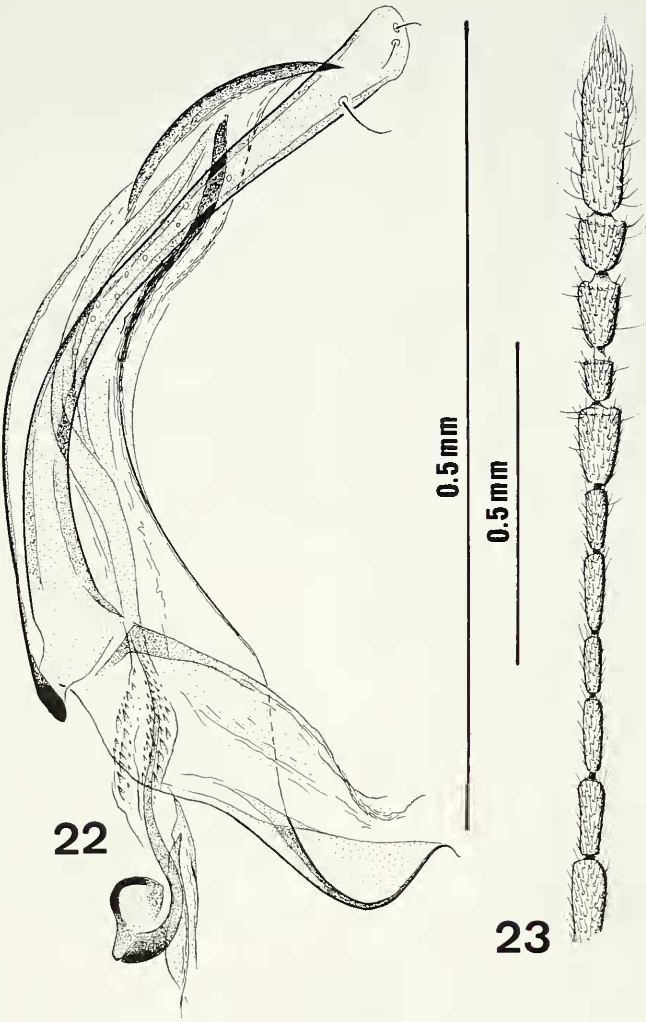
Figs 16-17
Lateral view of the aedeagus: (16) *Quaestus (Q.) jeannei* (Coiffait, 1965); (17) *Quaestus (Q.) recordationis* (Salgado, 1982).

the cave. From the biological perspective, this cave is of great interest as three troglobitic species of Leptodirini cohabit there: *Q. (Q.) longicornis*, *Q. (A.) incognitus* sp. n. and *Q. (S.) mermejaensis* sp. n., as well as *Notidocaris franzi* Jeannel, 1956, a musiculous species captured at the entrance. A very interesting member of the family Trechinae, *Apoduvalius* sp., morphologically very close to *A. espanoli* Salgado, 1996, is also found there.



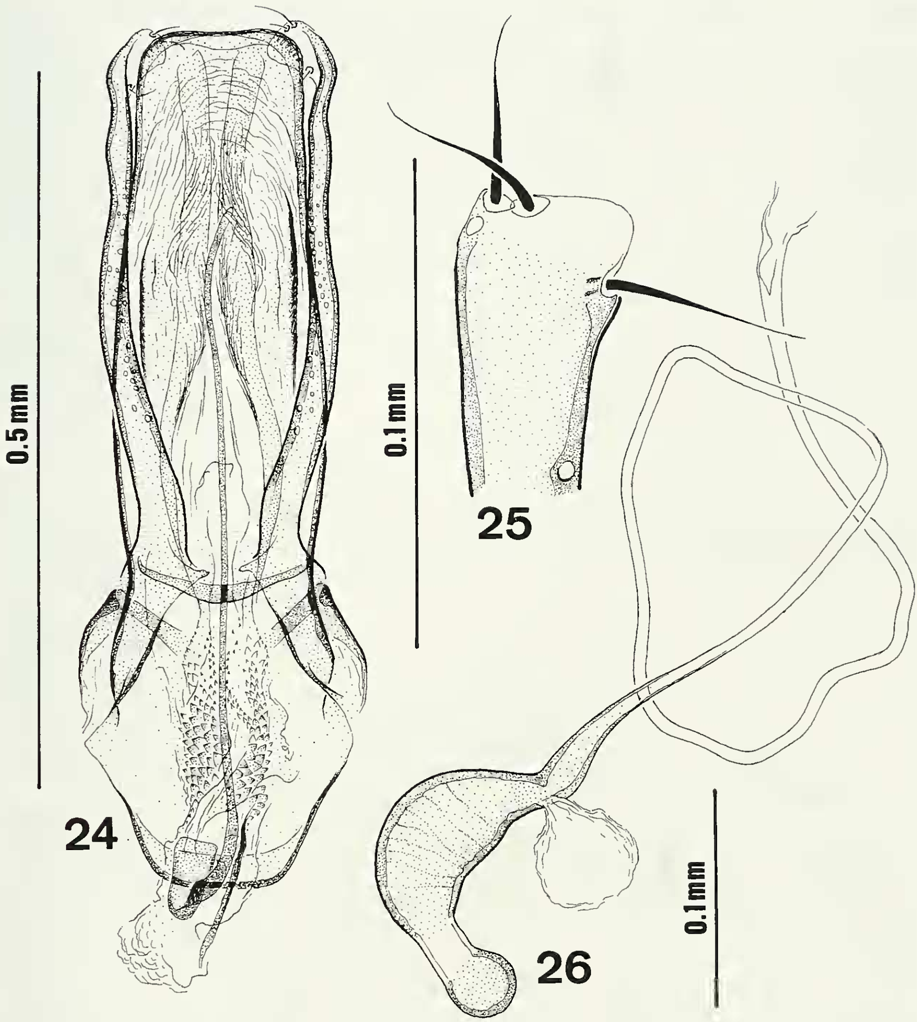
Figs 18-21

Quaestus (Speogeus) mermejaensis sp. n.: (18) aedeagus, dorsal view; (19) apical region of the paramere; (20) spermathecal complex; (21) mesosternal carina.



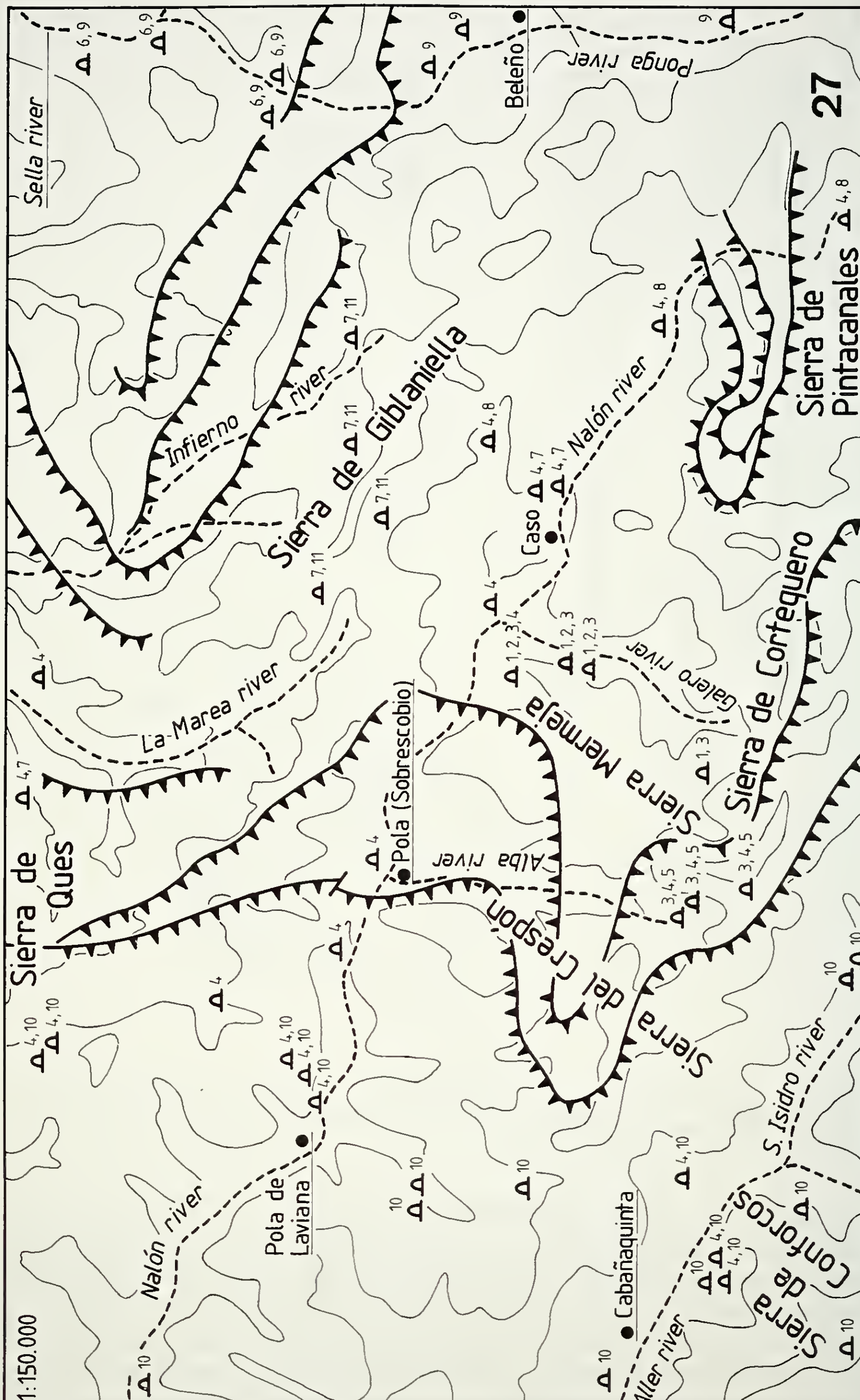
FIGS 22-23
Quaestus (S.) mermejaensis sp. n.: (22) aedeagus, lateral view; (23) antenna.

Carretera Cave (UTM: 30TUN056830). This cave is 400 m from the cave of the Prau. It is a small, very narrow gallery less than 25 m long. It is situated at 800 m alt. in limestone areas from the Carboniferous period. The entrance faces south-east, and is hidden mainly by *Sambucus nigra* L. and *Quercus robur* L. brambles and shrub branches. Because of its short length it is strongly influenced by atmospheric changes, so only a few specimens of *Q. (A.) incognitus* sp. n., *Q. (S.) mermejaensis* sp. n. and *Q. (Q.) longicornis* were captured using traps in the deepest parts.



FIGS 24-26
Quaestus (Speogeus) nietoi (Salgado, 1988): (24) aedeagus, dorsal view; (25) apical region of the paramere; (26) spermathecal complex.

Rearco cave (UTM: 30TUN054846). Of all the caves, this one is situated furthest north at an altitude of 650 m. As in the previous cases the limestone area where the cave was formed belongs to the Carboniferous period. The surrounding vegetation is *Crataegus monogyna* Jacq., *Corylus avellana* L., *Castanea sativa* L. and *Quercus robur* L. The cave was formed from a joint, producing a very narrow gallery leading into a larger chamber, 2 m high at the most and from which a network of very narrow low galleries lead off. The accessible area is approximately 175 m long. As the cave


27
1:150.000
Sella river
Beleño
Ponga river
Sierra de Pintacanales
Sierra de Giblaniella
Infierno river
Nalón river
Caso
Sierra de Cortequero
Galero river
La-Marea river
Pola (Sobrescobio)
Alba river
Sierra Mermeja
Sierra de Ques
Sierra del Crespón
Pola de Laviana
Nalón river
Cabañaquinta
S. Isidro river
Aller river
Sierra de Conforcos

entrance is very small, the physical factors are constant all the way through, with a temperature of 12° C and 98% relative humidity.

The fauna were captured in the first few meters inside the cave in organic plant matter, and in the rest of the cave in small heaps of organic animal material, especially bat faeces. The cave is of great biological interest because, to date, it is the only one in the world where 4 troglobitic species belonging to the same genus, *Quaestus (Q.) longicornis*, *Q. (Quaestus)* sp., *Q. (A.) incognitus* sp. n. and *Q. (S.) mermejaensis* sp. n. have been located, which is possible because they are all at different stages of evolution and have different microniches; for example, the two species belonging to the subgenus *Quaestus*, *Q. (Q.) longicornis* and *Q. (Quaestus)* sp., besides having completely different genitalia, the first species has clearly evolved more than the second because the appendices, legs and antennae are much longer and much more slender.

GEOGRAPHICAL DISTRIBUTION

As already pointed out the two new taxa *Q. (A.) incognitus* and *Q. (S.) mermejaensis* are found in caves in the eastern foothills of Sierra Mermeja and cohabit in the Prau, Carretera and Rearco caves. The two new species also cohabit with *Q. (Quaestus)* sp. and *Q. (Q.) longicornis* which is more widespread, though the morphological differences amongst them are very evident. Also, *Q. (S.) mermejaensis* has similar morphological characters to *Q. (S.) nietoi*, which inhabits a nearby karstic region and is much more widely distributed. It would be interesting to carry out a biogeographical analysis to obtain a better understanding of their genetic and geographical isolation in relation to the present distribution of the different species (fig. 27).

The various degrees of evolution may be considered as multistage processes in which several events occurred and gave rise to non-allopatric and allopatric speciation. Non-allopatric speciation occurred as a result of a diverging process of adaptation during the colonization of hypogeous environments by a population via gradual steps or stages with changes brought about by very different factors (Wilson, 1989; Bush, 1994). In the case of allopatric speciation, reproductive isolation was possible as a result of great climatic changes such as glaciation during the Pleistocene (Jeannel, 1942; Galán, 1993; Trajano, 1995) and the search for shelter (Bellés, 1987; Haffer, 1994), or the fragmentation of the habitat in isolated karstic areas (Bellés & Martínez, 1980; Reveillet, 1980; Salgado, 1995), which obviously occurred in this study area.

An examination of the species cohabiting in the caves described in this study, or morphologically proximate species inhabiting neighbouring areas, revealed that *Q. (Quaestus)* sp., which is very widespread, cohabits with *Q. (Speogeus) nietoi*, *Q. (S.)*

Fig. 27

Distribution map of the species: 1, *Quaestus (Asturianella) incognitus* sp. n.; 2, *Quaestus (Speogeus) mermejaensis* sp. n.; 3, *Quaestus (Quaestus) longicornis* (Salgado, 1989); 4, *Quaestus (Quaestus)* sp.; 5, *Quaestus (Speogeus) avicularis* (Salgado, 1985); 6, *Quaestus (S.) amicalis amicalis* (Salgado, 1984); 7, *Quaestus (S.) amicalis dilatatus* (Salgado, 1984); 8, *Quaestus (Q.) luctuosus* (Salgado, 1984); 9, *Quaestus (Q.) jeannei* (Coiffait, 1965); 10, *Quaestus (S.) nietoi* (Salgado, 1988); 11, *Quaestus (Q.) recordationis* (Salgado, 1982).

avicularis, Q. (S.) amicalis dilatatus, *Q. (Quaestus) longicornis*, *Q. (Q.) luctuosus*, and now with *Q. (S.) mermejaensis* sp. n. and *Q. (A.) incognitus* sp. n. in various caves. Of all the species mentioned, *Q. (Quaestus)* sp. is the least evolved, as shown by its morphological characters; the differentiating characters and genetic isolation may have occurred because the hypogeous environment was colonized in more recent periods. This theory is supported by the fact that the species is much more dispersed in karstic areas isolated by existing barriers which can be reached through the superficial underground compartment (MSS or Milieu Souterrain Superficiel, Juberthie *et al.*, 1981) as demonstrated by 3 catches recently made on the upper karst of Muñera (12-IX-1999), Pandanes (29-VI-2001) and Coballes (31-VII-2002).

Q. (Q.) longicornis is only known from the deep underground environment. Data on 3 caves in the Sierra del Crespón (Salgado, 1989) already existed and the 4 new ones from the Sierra Mermeja can now be added. Catches made in the caves show that there must have been a connection between the populations of these mountain ranges via fissures in the deep underground environment, the only way of establishing links between the populations of these fairly or very evolved species before the present barriers became established. The species cohabits with *Q. (S.) avicularis* and *Q. (Quaestus)* sp., in the Sierra del Crespon, with no impediments as they belong to different evolutionary stages, and in Sierra Mermeja with the two new taxons studied in this paper, and *Q. (Quaestus)* sp.

With regard morphological characters and proximity of colonization area, *Q. (S.) nietoi* is closest to *Q. (S.) mermejaensis* sp. n. Both belong to the same evolutionary stage and are therefore not found in the same area or cave. *Q. (S.) nietoi* is much more widely distributed than *Q. (S.) mermejaensis*, and is known from various caves in the karstic area between the Aller and Nalón river basins but limited by the Crespón, Mermeja and Ques sierras. At present both species are found in the deep underground compartment as they have never been located in the superficial underground environment through which they could migrate. Differentiation therefore occurred as a result of isolation by deep sandstone strata barriers and overthrusts which stopped the gene flow.

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